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Release and establishment of a biological control agent, *Psyllaephagus pilosus* for eucalyptus psyllid (*Ctenarytaina eucalypti*) in Ireland

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Summary

An Australian parasitoid wasp, *Psyllaephagus pilosus*, was collected from a previous release site in France and introduced into a commercial eucalyptus foliage plantation in Co. Kerry in the south west of Ireland to control the eucalyptus (blue gum) psyllid *Ctenarytaina eucalypti*. The first parasitised psyllid nymphs were observed 26 days after the release was made in late May 1998, and 49 days elapsed before a new generation of adult parasitoids was seen. Visually assessed indices of psyllid parasitism and adult wasp incidence were used to quantify the pattern of adult dispersion and establishment. A second generation of adult wasps emerged in late August, initiating a rapid spread of parasitism throughout the release site during September that culminated in a peak rate of almost 100% parasitism by late October. Subsequently by the end of 1998, an apparently random process of dispersion and successful natural colonisation occurred at eight out of ten monitored plantations at distances up to 70 km from the release point. The first colonisers of the other two sites arrived very late in 1998, and consequently failed to establish viable populations by the following summer. Probably this failure was because the small numbers of colonisers had arrived too late in the growing season to effect population establishment before the onset of winter. Assisted introductions were, therefore, made at these sites in June and August 1999, respectively. Once fully established, the parasitoid had no difficulty in surviving winter conditions at all monitored sites and demonstrated excellent potential as a biological control agent.

Key words: Biological control, insect parasitoid, *Psyllaephagus pilosus*, eucalyptus psyllid, *Ctenarytaina eucalypti*, eucalyptus foliage production, Ireland

Introduction

Originally an Australian species, the eucalyptus psyllid, *Ctenarytaina eucalypti* (Maskell) (Homoptera: Psylloidea: Spondyliaspididae) is now widely dispersed and a major pest of introduced eucalyptus species cultivated for amenity and commercial use throughout the world (Hodkinson, 1999*b*). Although Carne & Taylor (1984) mention having sent Australian chalcid parasitoids to Portugal and Spain in 1975 and 1976 to control the psyllid pest problem in those countries, there is no record of their establishment. The first biological control agent to be used successfully against the psyllid was an encyrtid wasp, *Psyllaephagus pilosus* (Noyes) (Hym. Encyrtidae). This species was collected from its native Australia, and after extensive quarantine testing, was first released in California, USA (Dahlsten *et al.*, 1993, 1996). Following this successful introduction, *P. pilosus* was released in a eucalyptus nursery in North Wales in the UK (Hodkinson, 1994) and in southern France (Malausa & Girardet, 1997) using specimens supplied from the original population quarantined in California. Although establishment in the relatively warm and dry climate of Mediterranean France was rapid and secured excellent biological control (Malausa, 1998), no detailed follow up study was done after the Welsh introduction. Observation of psyllid parasitism in commercial eucalyptus foliage plantations in Devon in the late 1990s (S Tones, personal communication) suggests that, not only was establishment achieved but the parasitoid had subsequently dispersed widely from the original release site. Whether this dispersal was entirely natural, or was assisted by the commercial trade in potted eucalyptus, is unclear and no assessment has yet been made of the influence of *Psyllaephagus* on psyllid pest incidence in the UK.

Five nymphal instars occur during the development of eucalyptus psyllid (Maskell, 1890). *P. pilosus* is a solitary endoparasitoid of the later nymphal instars (Dahlsten *et al.*, 1996). Like many such parasitoids (Quicke, 1997), the final larval parasitoid instar, when mature, chews a hole in its host's cuticle to allow fluids to escape and glue the shrivelled remains to the food plant, where the resulting 'mummy' serves to protect the pupating

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parasitoid inside. In addition to parasitising older psyllid nymphs, adult female wasps are effective predators that feed on younger nymphal instars by biting through their cuticle to lap haemolymph (Dahlsten *et al.*, 1996).

In this account, we report the release of *P. pilosus* in a commercial eucalyptus foliage plantation in Ireland, and document the process of parasitoid establishment, dispersion and colonisation of other commercial plantations throughout Co. Kerry.

Materials and Methods

Collection and release of P. pilosus

With the assistance of documentation regarding the previous importation and release of *P. pilosus* in California and Europe, a licence to release the parasitoid in Ireland in 1998 was granted by the Irish Department for Arts, Heritage, Gaeltacht and the Islands (Import Licence No. 64/67).

In preparation for release in the main area of eucalyptus foliage production, a shelter was erected at a commercial plantation near the village of Kilgarvan in early May 1998 (Fig. 1 - site KM1). The shelter, approximately 1.8 m high and 2 m diameter, was made from tent poles and nylon monofilament mesh (475 μm), and was constructed to completely enclose three psyllid-infested eucalyptus bushes and provide shelter from wind and rain.

Parasitised psyllid mummies on eucalyptus foliage and adult wasps were collected from a commercial plantation in the Alpes-Maritimes region (south east France) on the 19 and 20 May 1998. This French population had been established only the previous summer by release of individuals from the original quarantined population in California (Malausa & Girardet, 1997). Collected foliage, mummies and wasps were carefully screened in France and all other arthropods were removed prior to packaging and transportation by air within 72 h.

On 22 May 1998, approximately 2000 psyllid mummies and 180 adult wasps were placed in the shelter erected at KM1. Plastic lunch boxes containing foliage with French mummies were left open on the ground within the shelter and opened tubes containing adult wasps were suspended in the enclosed bushes. As a result of the modified environment inside the shelter, the psyllid population had developed more rapidly on the enclosed bushes compared with populations in the plantation as a whole. Consequently at the time of wasp release at the beginning of the Irish growing season, a greater proportion of psyllids inside the shelter were at the appropriate older nymphal stage to be parasitised. Purvis *et al.* (2002) provide specific details of weather conditions in the region in 1998, and an account of the influence of the climate in Co. Kerry on the seasonal incidence of the psyllid.

Assessment of parasitoid establishment

The rate of establishment and spread of parasitism was assessed in detail within a rectangular block of eucalyptus surrounding the release point. Within this 100 m × 60 m block, 58 bushes situated at the intersections of a 10 m × 10 m grid were individually marked. The release shelter was situated 30 m east and 20 m north of the south west corner of the grid, the direction from which the prevailing wind normally blows in Kerry.

Every week between the 18 June and the 29 October 1998, a non-destructive assessment of parasitoid incidence was made on the marked bushes. On each sampling occasion, 10 shoots were selected on the upper half of each bush without initial reference to their psyllid burden, and carefully searched and scored *in situ* for the presence of parasitised psyllid nymphs and adult wasps using scales of abundance described in Table 1.

An index of 'Relative Psyllid Parasitism' (RPP) for the total grid area was calculated at each assessment by determination of the ratio between the total sum of mean shoot scores per bush, and the maximum possible summed score that could be achieved if all sampled shoots returned the highest parasitism score (Table 1). Similarly, an index of 'Relative Adult Incidence' (RAI) was calculated on each sampling occasion from the sum of mean shoot scores for wasp incidence per bush (Table 1). This method was adopted because it was non-destructive, was considerably quicker and was probably more accurate than making actual counts in the field. Consequently, it permitted frequent and extensive assessment of the overall level and changing pattern of parasitoid incidence.

Maps of parasitoid incidence within the grid area were generated by curvilinear interpolation between mean shoot scores recorded at the fixed sample points using the 3-d surface chart facility of Deltagraph Professional® (SPSS Inc. Chicago) running on a Macintosh G4 microcomputer. For maximum clarity and a standardised presentation, each three-dimensional chart surface was edited by rotation to provide a shade-contoured, two-dimensional overhead view of parasitoid distribution.

Assessment of dispersion beyond the release site

During autumn and winter 1998, a total of 10 commercial eucalyptus plantations, distributed throughout the three main foliage-growing localities centred on the towns of Tralee, Killarney and Kenmare, were inspected weekly to document the first incidence of *P. pilosus* (Table 2, Fig. 1). Following the first detection of parasitism at a particular site, a programme of systematic monitoring at 2-wk intervals was adopted and continued until October 2000. On each sampling occasion, five stems were inspected on the upper half of each of 20 randomly selected bushes of *E. pulverulenta* and the incidence of nymphal parasitism and adult wasps was scored on scales described in Table 1.

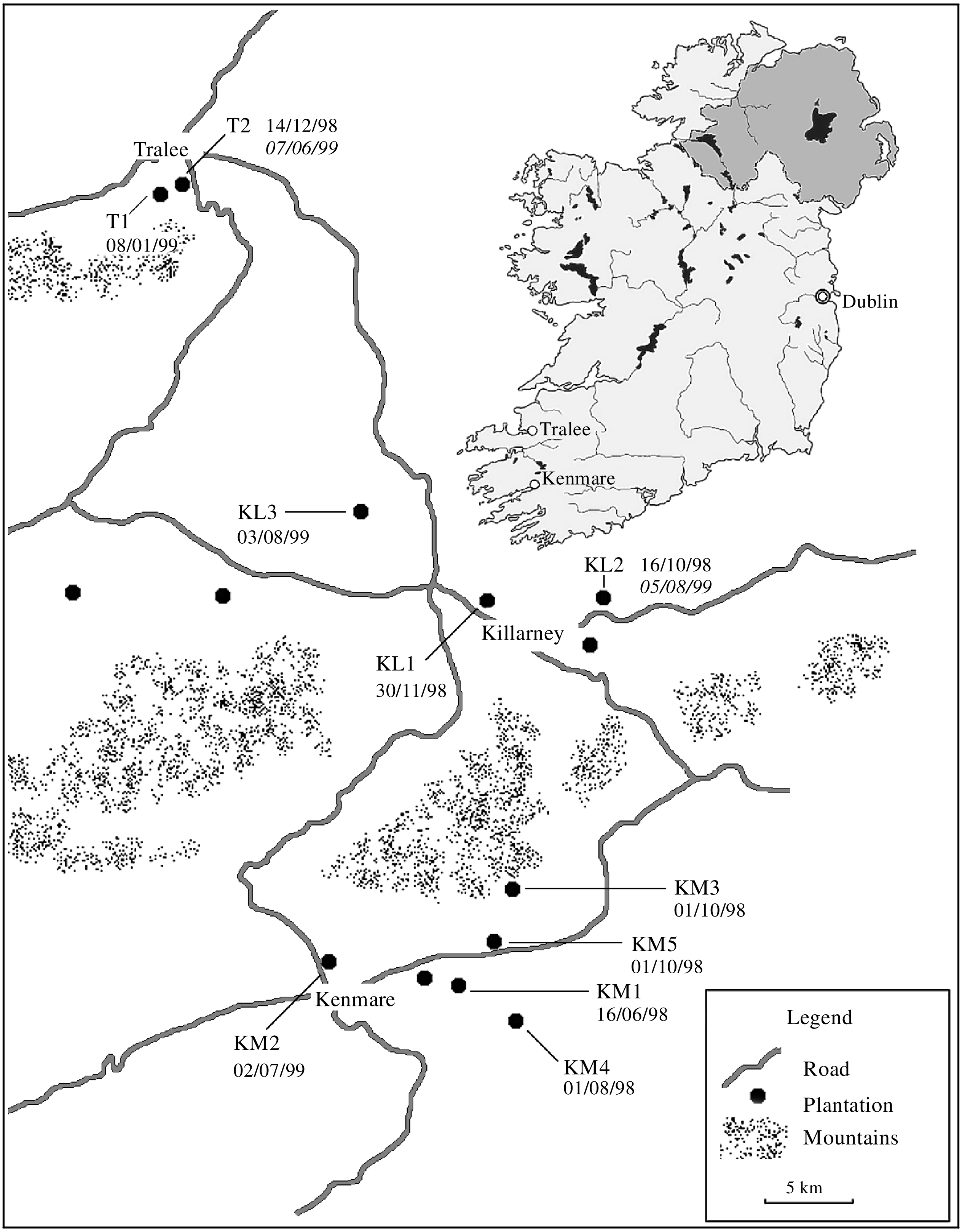

Fig. 1. Location of monitored plantations in Co. Kerry (south west Ireland) centred around the towns of Tralee, Killarney and Kenmare. *P. pilosus* was first released at site KM1 in the Kenmare region. Dates indicate the time of first incidence of natural colonisation; dates in italics indicate times of subsequent assisted introductions.

Table 1. *Shoot score methods used in the assessment of psyllid parasitism and the incidence of adult* P. pilosus

	Parasitism of older pigmented psyllid nymphs		Incidence of adult *P. pilosus*	
	Scale of nymphal parasitism on individual shoots	Index of Relative Psyllid Parasitism (RPP)	Scale of adult incidence on individual shoots	Index of Relative Adult Incidence (RAI)
Assessment of initial establishment within the sampling grid (58 bushes sampled)	Individual shoot scores: 0 - none parasitised 1 - individuals parasitised* 2 - colonies parasitised** 3 - all nymphs parasitised	$\frac{\Sigma\ p_i}{P_{max}}$	Individual shoot scores: 0 - none seen 1 - one adult 2 - two adults 3 - three-five adults 4 - > five adults	$\frac{\Sigma\ a_i}{A_{max}}$
	p_i mean shoot score per bush (n 10) P_{max} maximum possible sum of scores (58 î 3 174)		a_i mean shoot score per bush (n 10) A_{max} maximum possible sum of scores (58 î 4 232)	
Assessment of subsequent dispersion and colonisation of sites (20 bushes sampled per site)	Individual shoot scores: 0 - none parasitised 1 - one nymph parasitised 2 - individuals parasitised* 3 - colonies parasitised** 4 - unparasitised nymphs only on terminal bud 5 - all nymphs parasitised 6 - shoot with no pigmented nymphs	$\frac{\Sigma\ p_i}{P_{max}}$	Individual shoot scores: 0 - none seen 1 - one adult 2 - two adults 3 - three-five adults 4 - > five adults	$\frac{\Sigma\ a_i}{A_{max}}$
	p_i mean shoot score per bush (n 5) P_{max} maximum possible sum of scores (20 î 6 120)		a_i mean shoot score per bush (n 5) A_{max} maximum possible sum of scores (20 î 4 80)	

* individually parasitised nymphs widely distributed throughout the shoot, less than 15 on any single leaf node
** at least one colony of 15 or more nymphs on the same leaf node all parasitised

Table 2. *Description of plantations in which the incidence of* P. pilosus *was routinely monitored between December 1998 and October 2000*

Region	Site	Location	Area (ha)	Aspect	Planting date	*Eucalyptus* spp.*	Distance from release site (km)
Kenmare:							
	KM1	Lat. 51 54' N Long. 09 30' W	6.4	North facing	1994/1998	gl, mo, pa, pu	0
	KM2	Lat. 51 54' N Long. 09 36' W	0.4	South facing	1994	gl, pu	8
	KM3	Lat. 51 55' N Long. 09 29' W	1.8	Level	1994	gl, pu	10
	KM4	Lat. 51 51' N Long. 09 25' W	1.8	East facing	1993	gu, pe, pu	7
	KM5	Lat. 51 54' N Long. 09 28' W	0.6	Level	1993	gl, mo, pa, pu	3
Killarney:							
	KL1	Lat. 52 04' N Long. 09 30' W	8.0	South facing	1995	gl, pa, pe, pu	32
	KL2	Lat. 52 03' N Long. 09 24' W	1.8	South facing	1994	gl, pa, pe, pu	35
	KL3	Lat. 52 07' N Long. 09 32' W	1.4	East facing	1996	pe, ru**	37
Tralee:							
	T1	Lat. 52 14' N Long. 09 43' W	1.2	Level	1994	gl, pu	70
	T2	Lat. 52 15' N Long. 09 41' W	1.8	Level	1994	gl, mo, pu	70

* Eucalyptus species: gl, *E. glaucescens*; gu, *E. gunnii*; mo, *E. moorei*; pa, *E. parvifolia*; pe, *E. perreniana*; pu, *E. pulverulenta*; ru, *E. rubida*
** In the absence of *E. pulverulenta*, plants of both these species were randomly sampled

Assisted dispersion

By mid-summer 1999, it became obvious that *P. pilosus* had not fully established at KL2 and T2 (Fig. 1). Assisted introductions were then made at these sites by collecting foliage bearing psyllid mummies from successfully colonised plantations and placing it in buckets of water at two-three strategic locations within the uncolonised plantations and by collecting and releasing adult wasps using an insect aspirator.

Results

Parasitoid establishment at Kilgarvan

The release shelter was visited daily following the original introduction. Major milestones in the establishment process are listed in Table 3. Initially, released adults were observed searching shoots within the shelter for psyllid hosts. After 3 days, it was decided that there had been sufficient opportunity for parasitism within the shelter and the mesh cover was removed to allow dispersal within the wider plantation. Temperatures at this time dropped to a minimum of 8°C at night. Despite this, adult wasps continued to emerge from the imported mummies on a daily basis. Very heavy rainfall (Purvis *et al.,* 2002) became the cause of significant mortality amongst emerging adults as rain and condensation collected within the release boxes. In an attempt to minimise these losses, a decision was taken on 2 June to empty the remaining contents of the boxes onto the open ground. At this time, observations showed that most wasps were sheltering motionless under the protection of foliage, despite the ready availability of psyllid hosts. This contrasted markedly with experience in southern France, where released wasps foraged openly and continuously on stems for unparasitised hosts (J-C Malausa, personal communication).

By mid-June, the first parasitised 'Irish' psyllids were found on the original release bushes. Initially, numbers were small and individually distributed within colonies of healthy psyllid nymphs. Adult wasps were becoming more difficult to find. The numbers of evidently parasitised psyllid nymphs steadily increased on the release bushes and on the 22nd June, the first completely parasitised colony of nymphs (> 15 on the same leaf node) was found. Parasitised nymphs were not seen on bushes outside the original enclosure until the end of June, when they could be found at distances of up to 5 m from the release point. On the 8th July, 49 days after the original release, the first empty 'Irish' psyllid mummies were found on the release bushes indicating the beginning of emergence of a new adult generation.

Spread of parasitism at Kilgarvan in 1998

The incidence of parasitism remained low and largely confined to the release area until mid-August, when an exponential increase began culminating in a peak RPP index of 0.989 for the entire grid area in late October 1998 (Fig. 2). Sightings of adult wasps remained similarly restricted until the 20 August, when the emergence of a major new adult generation began and peaked with a maximum RAI index in late September 1998 (Fig. 2). Subsequently, adult wasp numbers declined in early October before a second, much smaller peak in incidence was recorded in mid-October.

The detailed pattern of increasing psyllid parasitism and adult wasp incidence throughout 1998 is shown in Figs 3 and 4, respectively. Parasitism spread throughout the grid in a predominantly easterly direction matching the prevailing wind

Table 3. *Establishment milestones following the original placement of adult* P. pilosus *wasps and opened boxes containing parasitised psyllid nymphs in a shelter covering three eucalyptus bushes at site KM1 on 22 May 1998*

Days after release	Event
3	Shelter opened to allow wider dispersion by released adults
10	Remaining French foliage emptied onto the ground following heavy rain-induced mortality of emerging adults within boxes
26	First individual parasitised nymphs noted on bushes within the original shelter
33	First shoots with completely parasitised colonies of nymphs recorded on bushes within the original shelter
49	First emergence of adult wasps from 'Irish' psyllids on bushes within the original shelter

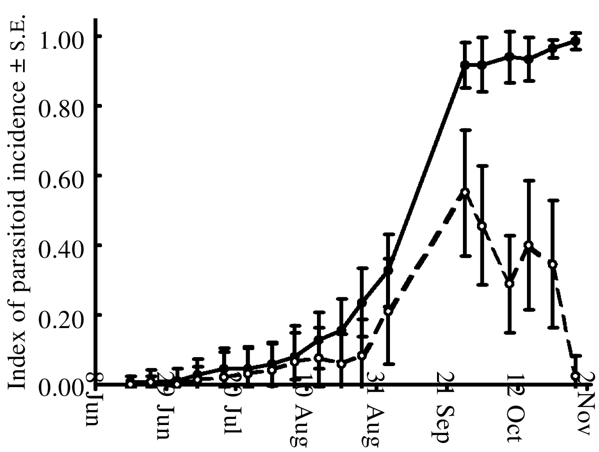

Fig. 2. Mean incidence of a) *P. pilosus* mummies (RPP index) and b) *P. pilosus* adults (RAI index) within the intensively sampled grid following the release of parasitoids at site (KM1).

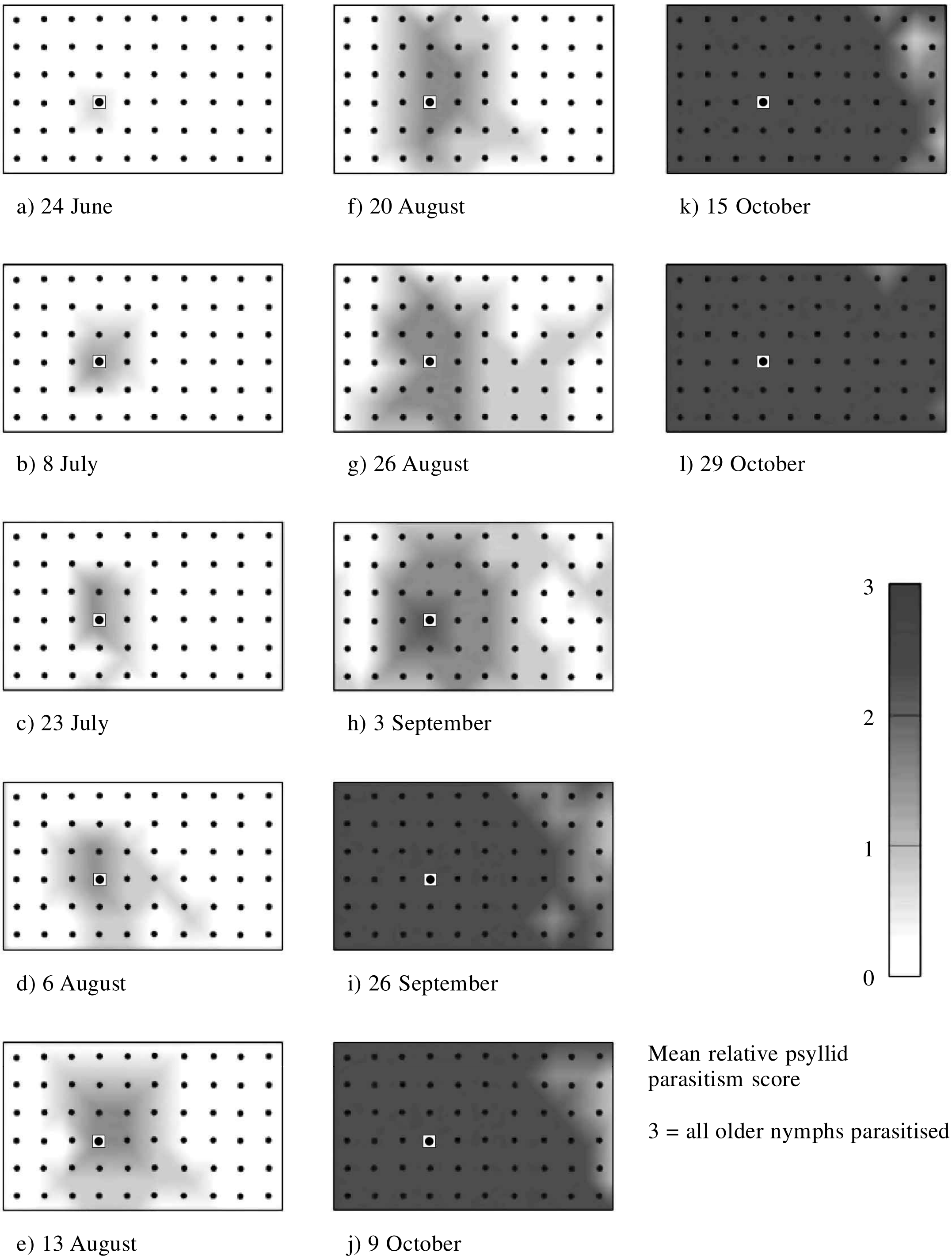

Fig. 3. Distribution of nymphal psyllid parasitism throughout the intensively sampled release area at site KM1. Black dots represent repeatedly sampled plants on a 10 m × 10 m grid pattern; the open square indicates the point of release.

direction from the south west. By the end of October, unparasitised older nymphs could be found only in very small numbers at the eastern end of the grid. Adult wasp incidence in the vicinity of the release point increased markedly during early September, after which wasps dispersed widely throughout the grid (Fig. 4). By the end of October, adult wasp activity was restricted to the eastern end of the grid where small numbers of unparasitised hosts could still be found.

Dispersion beyond the release site

The first parasitised psyllids seen outside the original release site were found 7 km away at KM5 on 1 August 1998 (Fig. 1). By early October 1998, parasitism had been observed at KM3, KM4 and KM5. The last site to be naturally colonised in the Kenmare area was KM2 where the first parasitised nymphs were not found until 2 July 1999, 13 months after the original release. In the Killarney area, more than 30 km from the introduction, KL1 and KL3

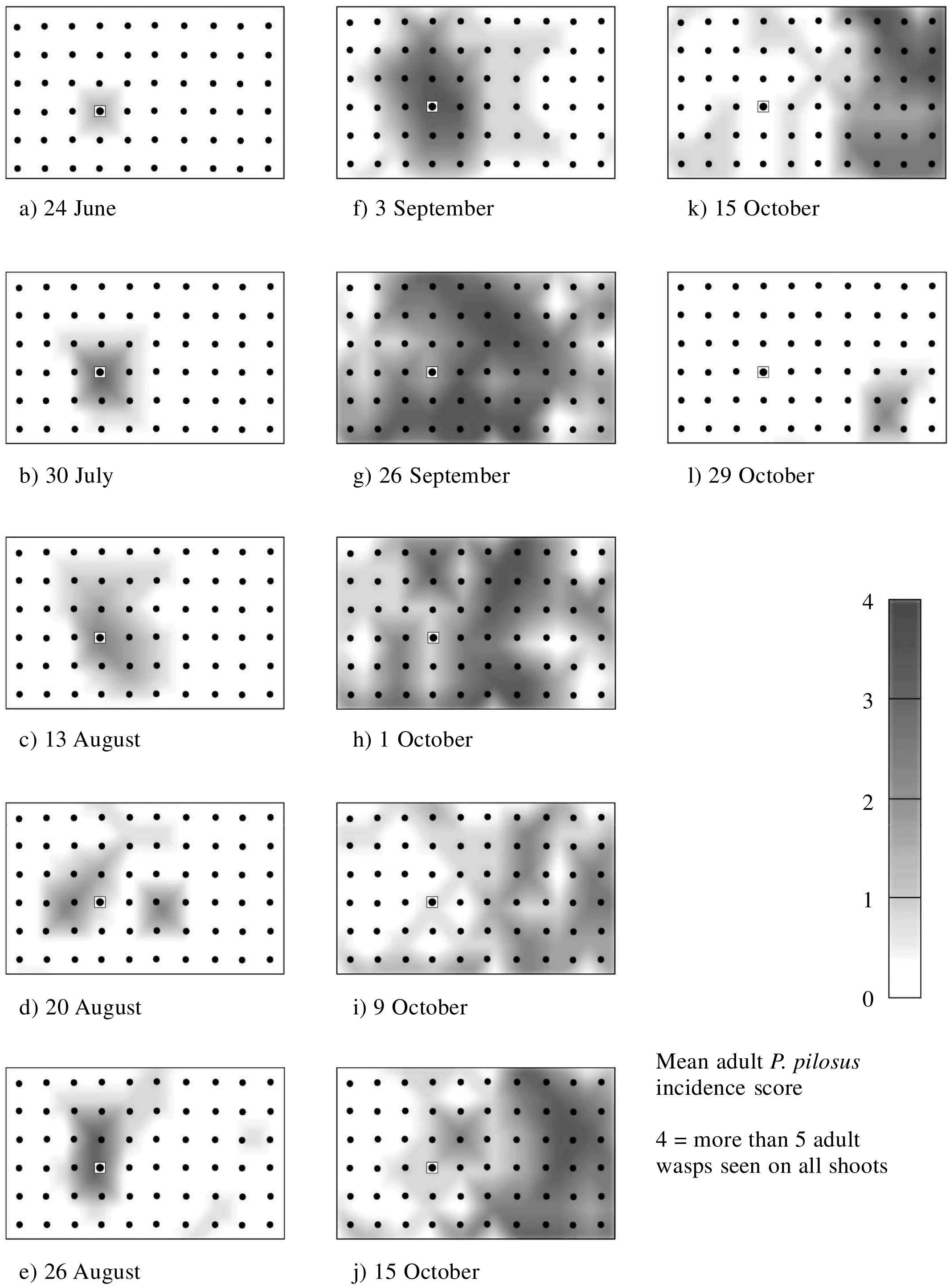

Fig. 4. Distribution of adult *P. pilosus* throughout the intensively sampled release area at site KM1. Black dots represent repeatedly sampled plants on a 10 m × 10 m grid pattern; the open square indicates the point of release.

were colonised by late November 1998, but at KL2 the first evidence of parasitism was not seen until early August 1999. Consequently to ensure effective establishment in 1999, an assisted release was made at this site later in the same month. In the Tralee area, at a distance of more than 70 km from the release, parasitism was first seen at T2 in December 1998, but not before early January 1999 at T1. By June 1999, it had become apparent that the first colonisers at T2 had failed to survive the winter and an assisted introduction was made at this site in July of that year.

Development of parasitism throughout Kerry

The RPP index for the wider release site (see Table 1) reached 0.75 by December 1998 (Fig. 5a). The site index subsequently increased further in 1999 and reached a maximum possible value of 1.00 by September, when all potential hosts on sampled shoots were parasitised. During the subsequent

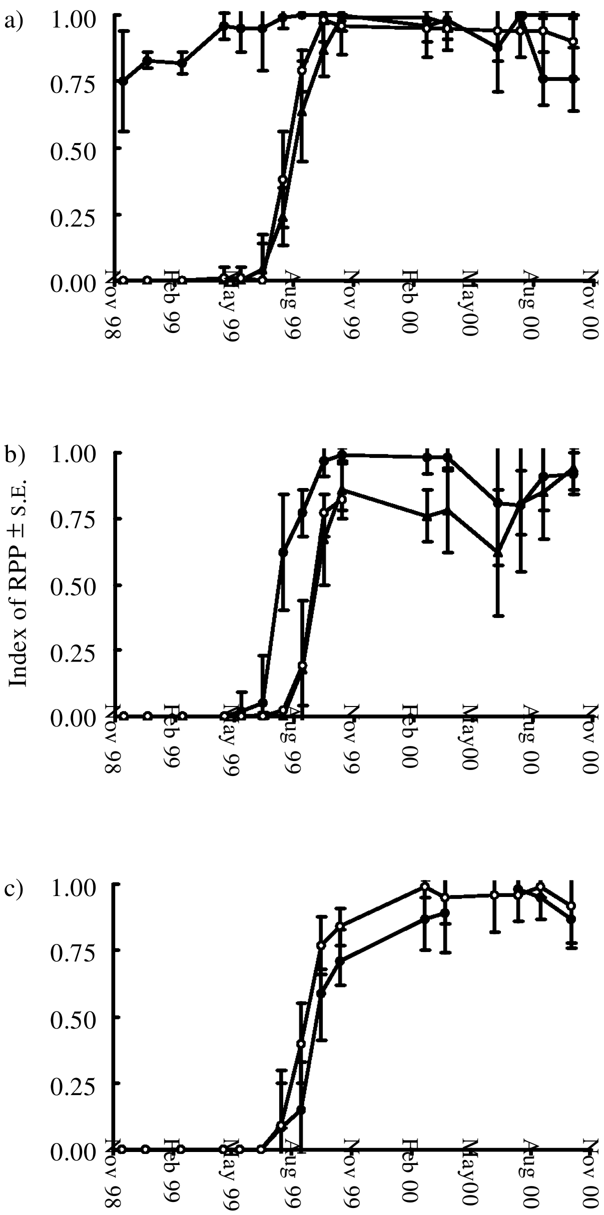

Fig. 5. Incidence of psyllid parasitism (RPP index) at monitored plantations throughout Co. Kerry:
a) Kenmare, (KM1, ● ; KM2, ▲; KM3, ○)
b) Killarney, (KL1, ● ; KL2, ▲; KL3, ○)
c) Tralee regions, (T1, ● ; T2, ○).

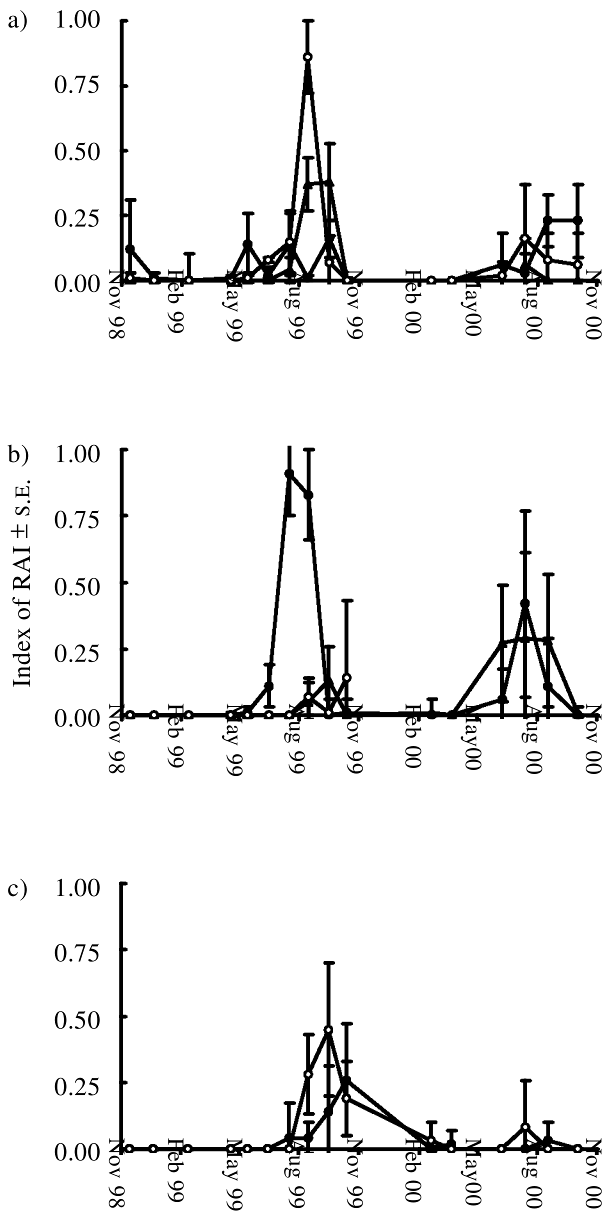

Fig. 6. Incidence of adult wasps (RAI index) at monitored plantations throughout Co. Kerry:
a) Kenmare (KK1, ● ; KK2, ▲; KK3, ○)
b) Killarney (KL1, ● ; KL2, ▲; KL3, ○)
c) Tralee regions (T1, ● ; T2, ○).

winter, small numbers of eggs, but no active psyllid instars, were found. In the following summer, the psyllid population was re-established after pruning by oviposition on foliage re-growth. Parasitism however remained high, the RPP index reached a maximal value of 1.00 again in August 2000, before falling to 0.76 in September and October. Throughout 1999 and 2000, the incidence of adult wasps at KM1 remained relatively low with only minor peaks in the RAI index recorded in June, August and October 1999, and in July and September-October 2000 (Fig. 6a).

During 1999, the level of parasitism at KM2 and KM3 was initially very low (Fig. 5a). A minor peak in adult wasp incidence was recorded in early July and a second, much larger peak occurred in September (Fig. 6a). This led to a dramatic increase in nymphal parasitism from late July onwards as the parasitoid became widely established and the parasitism index peaked at 0.99 and 0.98, respectively, in October/November. In March 2000, and throughout the subsequent growing season, the level of nymphal parasitism at KM2 and KM3 remained high (RPP > 0.87). In comparison to the previous season, however, few adult wasps were seen with minor peaks in incidence recorded during late July-August 2000.

At KL1, nymphal parasitism increased markedly in July 1999, 2 months earlier than at KL2 or KL3 (Fig. 5b). Maximum parasitism at KL1 was recorded in October 1999 (RPP = 0.97) and remained at a high level until the crop was pruned in April 2000. Pruning resulted in a marginal decrease in the parasitism index as psyllid populations recovered on new foliage growth. Subsequently, very high levels of parasitism were again achieved by October 2000 (RPP = 0.92). Numbers of adult wasps at KL1 in 1999 (the year of establishment) reached a very substantial peak in late July-August but much lower numbers were seen in 2000 (Fig. 6b).

Nymphal parasitism at KL2 and KL3 remained lower than KL1 throughout 1999, but followed a similar sigmoidal pattern with peak indices of 0.86 and 0.92, respectively, recorded in early November (Fig. 5b). Sampling at site KL3 stopped at this point when the grower disposed of his crop. Throughout the 1999/2000 winter, nymphal parasitism at KL2 remained less than at KL1; a difference that continued during most of the following growing season. A minimum parasitism index of 0.62 was recorded at KL2 in June 2000, at a time of psyllid population resurgence following crop pruning. From this minimum level, nymphal parasitism steadily increased at KL2, to reach a peak index of 0.94 in October before the end of the growing season. In contrast to KL1, few adults were seen during the entire 1999 growing season at KL2 and KL3; minor peaks in the adult index being recorded only relatively late in October and November, respectively (Fig. 6b). Observations at KL2 in 2000 showed a relatively prolonged period of adult wasp activity during July-September.

The development of parasitism at T1 and T2 followed a similar, strongly sigmoidal pattern in 1999 with a marked increase occurring in August/September (Fig. 5c). At T1, this was a natural process, but at T2 it had only followed an assisted introduction in July. Adult wasp incidence at T1 and T2 peaked relatively late in September-October 1999 (Fig. 6c). In 2000, high levels of nymphal parasitism were documented throughout the season at both Tralee sites (RPP = 0.83 - 0.99) (Fig. 5c), however, only very small numbers of adult wasps were seen during sampling with the RAI index peaking in July-August 2000 (Fig. 6c).

Discussion

Initial establishment

The mortality rate of *Psyllaephagus* adults, especially during emergence from imported mummies, was much higher than expected in unusually wet weather conditions during the first 2-3 wk following release. Despite these adverse circumstances, however, a sufficient number of wasps survived to begin the process of parasitism and successful establishment. The first observation of empty 'Irish' psyllid mummies, however, suggested a considerably longer generation interval than that recorded following releases in California and south east France, where *P. pilosus* was able to produce multiple generations in the season of release (Dahlsten *et al.*, 1998; Girardet, 1997). In the laboratory, *P. pilosus* can complete a generation in only 3 wk at 25°C (Dahlsten *et al.*, 1998). Following release in Wales in climatic conditions similar to Kerry, 32 days elapsed before the first locally parasitised psyllid nymphs were found, and evidence of a new generation of adult wasps was only found after 68 days (Hodkinson, 1999*a*).

Dispersal from the release point

Numerous behavioural experiments have demonstrated the tendency for parasitoids to leave the immediate vicinity after an encounter with a conspecific, an already parasitised host, or a chemical parasitoid marker deposited by other females after oviposition (Jervis & Kidd, 1996). However for a considerable time following release, the distribution of both adult wasps and nymphal parasitism remained restricted to the immediate vicinity of the release bushes. The weather almost certainly deterred normal host-finding behaviour but the prolonged delay before significant dispersal also suggests that wider foraging was inhibited until an exhaustion of the local supply of suitable hosts forced female wasps to leave the release area. The emergence of a major new adult wasp generation beginning in August appeared to substantially increase competition for hosts and trigger the wider establishment of parasitism throughout the release site from September onwards.

The life cycle of P. pilosus *in the year of release*

In view of the pattern of adult incidence with peaks observed in August, late September and mid-October (Fig. 2b), it is probable that at least two generations of wasps, and possibly a partial third, were produced before the onset of winter. There is a possibility that at least some of the variation in observed adult incidence was a sampling artefact caused by variable adult apparency. The visability of adult wasps in the field was certainly reduced in wet and heavily overcast conditions as normal foraging behaviour was inhibited and wasps sought shelter amongst foliage. Aware of this possibility, sampled stems were very careful searched on all occasions. It is therefore likely that observed peaks in numbers reflected real changes in actual abundance, and these peaks may be explained by the original release of both adult wasps and parasitised psyllid nymphs. The former began parasitising nymphs more or less immediately. In contrast, introduced immature parasitoids had to complete their larval and pupal development in less than ideal climatic conditions before they could begin to contribute to the next generation. Consequently, two temporally distinct wasp cohorts may have developed from the introduced wasp population, which might explain the bimodal adult activity pattern seen in September and October. If an estimate of 49 days is applied to the likely development of a second wasp generation beginning with an oviposition peak in early August, a further generation of adults would be expected to appear in late September. This is consistent with observations (Fig. 2b). A delay of several weeks in oviposition by wasps that emerged from imported mummies, might then explain the subsequent peak in adult numbers seen in mid-October. Alternatively, this later peak may represent the emergence of a partial third generation of wasps, which may have been achievable with the earliest oviposition occurring before the end of May and a mean generation interval of 40-50 days.

The wider dispersal abilities of P. pilosus

Dispersal over distances of up to 70 km between plantations was achieved within the first season of release. This is consistent with experience elsewhere. In south east France, following initial release in June 1997, *P. pilosus* dispersed widely reaching the island of Porquerolles (Var) situated 85 km west of the release point after only 8 months (Malausa & César, 1998). In much of France, eucalyptus is a common urban and suburban tree widely planted on roadsides and in gardens, and this undoubtedly assisted the rapid spread of the wasp between commercial plantations. In contrast, there is little or no eucalyptus grown in Kerry outside the network of widely scattered and relatively small commercial foliage plantations. Despite this lack of assistance, small numbers of parasitised psyllid nymphs were found at the majority of monitored plantations by the end of the first growing season. It is reasonable to assume that colonisation of these distant sites did not begin before September-October, when large numbers of a second wasp generation at the release site were probably forced to disperse because of a dramatic reduction in host availability.

Two distinct phases in parasitoid host finding behaviour have been recognised: location of the host's habitat and location of the host within its habitat (Jervis & Kidd, 1986). Highly host specific parasitoids frequently use host plant chemistry in the location of an appropriate habitat, and then use the complex of interactions between the insect host and its food plant to assist in the second stage of host location (Hassel & Waage, 1984; Godfray & Shimada, 1999). *Eucalyptus* species contain a diverse and strongly pungent range of essential oils and phenolics that might be expected to provide powerful initial orientation cues. The sequence of colonisation at sites throughout Kerry, however, suggests that the process of finding new plantations may have been largely a question of chance. At two sites, KM2 in the immediate area of release, and KL3 in the adjacent Killarney area, no evidence of colonisation was found in the first year, but parasitoids were found at both locations in the more remote Tralee area (see Fig. 1). The sequence of arrival was, therefore, not strongly correlated with distance from the colonising source and suggests that a large element of chance and probably only a small number of wasps were involved in initial colonisation.

The high rate of successful establishment achieved by this small number of initial colonists suggests that the fecundity of the wasp is high and the process of host location on its food plant is extremely efficient. In fact, establishment was so successful that it was only necessary to supplement the process at two out of 10 sites. These failures resulted, not because the sites were not found, but probably because they were found only very late in the growing season.

Measuring parasitism

Non-destructive scoring techniques were developed and used in the current study to document the first incidence and subsequent relative levels of parasitism. This approach was necessary because of the initial scarcity of parasitoid populations at newly colonised sites, and the need not to jeopardise parasitoid establishment. However, it would be misleading to regard the indices used as equivalent to a precise estimation of the actual rate of parasitism. This requires accurate determination of the overall proportion of parasitised hosts, which may only be possible by dissection if the earliest stages of parasitism are not externally evident (Van Driesche, 1983). Even without dissection, accurate visual counts in the field at very high psyllid densities would have been massively time consuming and logistically impossible at multiple sites. An accurate assessment of the rate of parasitism is desirable, however, for any detailed evaluation of the impact of a parasitoid on its host population (Bellows *et al.*, 1992). Nonetheless, the methods used permitted an accurate quantification of the relative incidence of parasitism in the host population, to the point when all suitable hosts were evidently parasitised. In the latter regard, psyllid nymphs can be readily categorised visually in the field as 'younger' first and second instars are unsclerotised and bright yellow in colour whilst 'older' third-fifth instars are light beige in colour with evidently darker dorsal sclerites. Throughout observations in the field, only the latter sclerotised instars were seen to be parasitised when the body became obviously swollen and darkly discoloured. The scoring scale was devised to quantify the *relative* level of parasitism in these older nymphs. Initially, psyllid numbers were very high at all sites before the establishment and spread of *P. pilosus*. Maximum parasitism scores were recorded when all potential host nymphs were seen to be parasitised, and continued to be recorded for as long as unparasitised older nymphs remained absent. At this point, as large numbers of wasps emerged from mummies, often only psyllid eggs and young nymphs could be found on sampled shoots. On inspection under the microscope, many of the remaining young nymphs were found to be dead – presumably as a result of predation by adult wasps (Dahlsten *et al*., 1996). Therefore by continuing to record maximum parasitism scores in the absence of unparasitised older nymphs, the parasitism index effectively became an empirical measure of psyllid control.

Impact on psyllid numbers

In contrast to the successful dispersion to new sites, the relative rate of increase in parasitism within sites was relatively much slower in Ireland compared to experience elsewhere. In the south east of France, parasitism of suitable nymphal instars reached 100% within 3 months of introduction (Girardet, 1997). In Brittany, in western France, where *P. pilosus* was independently introduced in October 1997, parasitism levels of at least 98% were reached, only 9 months later (Malausa & César, 1998). By contrast, because of the extended duration of development in Ireland, the parasitoid took a whole growing season to complete at least two full generations. Encouragingly, in all monitored plantations and years of the study, the second wasp generation effected very high levels of psyllid parasitism (94-100%) and a high level of pest control was achieved by the time of stem harvesting at the end of the growing season. This invariably resulted in much lower incidence of both host and parasitoid in the second season after establishment. Despite this, the parasitoid had no apparent difficulty in surviving the Irish winter, even at the relatively low absolute population levels that prevailed from the second year after establishment. Further population studies will be required to confirm the reliability of psyllid population control by the time of foliage harvesting in late autumn, and only experience of climatically variable seasons will show whether effective psyllid control is possible without careful crop management. In particular, control of the method and timing of stem harvesting in autumn, and the extent and date of pruning in spring, may prove necessary to guarantee cosmetically clean crops by the end of the growing season. Results to date, however, demonstrate the viability of *P. pilosus* in temperate climatic conditions and indicate that the parasitoid has excellent potential as a biological control agent that can obviate the need for pesticide use in commercial plantations.

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